BALLOONING MYGALOMORPHS: ESTIMATES OF THE MASSES OF *SPHODROS* AND *UMMIDIA* BALLOONERS (ARANEAE: ATYPIDAE, CTENIZIDAE)

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ABSTRACT

The masses of *Sphodros atlanticus* and *Ummidia* sp. spiderlings capable of ballooning, and of *Antrodiaetus unicolor* spiderlings believed not to balloon, were estimated by means of a volume-mass regression developed with data from five araneomorph families, and compared with the mass frequency distribution of a sample of 216 aerially dispersing araneomorphs trapped over a one week period in a soybean field. Mean estimated masses of the *Sphodros* and *Ummidia* spiderlings were 1.25 mg and 3.45 mg, respectively. Although these were in at least the 95th percentile of masses of the trapped araneomorphs, larger araneomorphs were trapped. These results and the finding that *A. unicolor* spiderlings were intermediate in estimated mass (mean = 2.02 mg) between *S. atlanticus* and *Ummidia*, indicate that mass is not the only constraint on ballooning behavior in mygalomorphs. Habitats of the three species support the habitat predictability hypothesis of ballooning, *A. unicolor* tending to be found in more predictable habitats than the other two species. Live mass measurements of ballooning *Ummidia* spiderlings indicate that the volume-mass regression estimates of mygalomorph spiderling masses are consistently slightly high. This may be due to tissue density differences between araneomorphs and mygalomorphs.

INTRODUCTION

Although the great majority of mygalomorph spider species do not appear to disperse aerially, observations of ballooning *Sphodros atlanticus* (Gertsch and Platnick) and *Ummidia* spiderlings (Coyle 1983, 1985) and of pre-ballooning behavior in spiderlings of *Sphodros rufipes* (Latreille) (Muma and Muma 1945), *Atypus affinis* Eichwald (Enock 1885, Bristowe 1939), *Ummidia carabivora* (Atkinson) (Baerg 1928), and *Conothele malayana* (Doleschall) (Main 1957) show that some species in two mygalomorph families (Atypidae and Ctenizidae) are aerial dispersers. Although *Sphodros* and *Ummidia* ballooning (which involves dropping and hanging from a dragline that is lifted and lengthened by a breeze,

breaks near the attachment substrate, and serves as the ballooning thread) is a more primitive (and probably less effective) form of ballooning than that practiced by most araneomorphs, it appears to increase significantly the vagility of these animals (Coyle 1983). The water gaps bridged by the distribution ranges of *A. affinis* (Kraus and Baur 1974; Locket, Millidge, and Merrett 1974), *C. malayana* (Main 1957), and by other *Atypus* and *Ummidia* species in Japan (Yaginuma 1970) and the Florida Keys (G. B. Edwards, pers. comm.) also suggest that mygalomorph ballooning can significantly increase vagility.

Because spiders are not capable of active flight, there must be some upper limit to the mass at which they can disperse aerially. Ballooning in mygalomorphs has therefore been an arachnological curiosity, since average mygalomorph adults and spiderlings (data presented in this paper) are far more massive than the corresponding stages of araneomorphs. This study was designed to estimate the masses of ballooning mygalomorph spiders and to compare them with the masses of typical ballooning araneomorphs, so that the following questions can begin to be addressed: is ballooning rare in mygalomorphs primarily because of large spiderling size? In those mygalomorph species which do balloon, to what degree is large mass a handicap which has been overcome by special adaptations?

METHODS AND STUDY SITES

Sphodros atlanticus spiderlings were collected on 9 October 1980 with their mother in her burrow on a grassy roadbank 6.5 km south of Cullowhee in Jackson County, North Carolina. These were third instar spiderlings which overwinter in the maternal burrow and disperse in the spring (see Coyle and Shear 1981, for a description). Spiderlings of an undetermined species of *Ummidia* were collected while performing pre-ballooning behavior (climbing around in the top of a boxwood shrub about 1 m above ground) on 19 April 1982 near Apex in Wake County, North Carolina, by J. M. Ragan. Twenty dispersal stage (second instar) spiderlings of *Antrodiaetus unicolor,* collected on 16 January 1973, eight km south of Cullowhee in Jackson County on the Wolf Creek Biological Preserve, were included in the study to provide mass estimates for a mygalomorph which is believed not to balloon (Coyle 1971, Reagan and McGimsey pers. comm.). All spiderlings were preserved in 70% ethanol.

Ballooning araneomorphs were collected on vertical sticky traps set out between 30 and 200 cm high in an eleven ha. soybean planting at the University of Missouri South Farms, eight km SE of Columbia in Boone County, Missouri, during the seven-day period ending 9 August 1983. Details of the trapping procedure have been presented elsewhere (Greenstone 1984). Briefly, the trap supports were banded with adhesive to prevent spiders from walking onto them, and all vegetation was cleared from within 3 m of the traps to reduce the probability that spiders would be inadvertently trapped while "rappelling" (J. E. Carico, personal communication) or "bridging", i.e., floating silk "lines on the wind to establish paths to distant objects" without releasing hold of the substrate (W. G. Eberhard, personal communication). The traps were returned to the laboratory and examined with a Wild M5 stereomicroscope to locate all trapped spiders. The spiders were removed from the adhesive (Tacktrap®, Animal Repellents, Inc., Tifton, Ga) and placed for three days each in paint thinner and toluene before final preservation in 70% ethanol.

Mass estimates for both the mygalomorphs and sticky-trapped araneomorphs were made by use of a volume-mass regression developed with 101 araneomorph specimens ranging in mass from 0.7 to 19.5 mg. Briefly, previously massed animals were preserved in 70% ethanol and their volume estimated by treating them as cylindrical solids having diameter equal to the mean of greatest carapace and abdominal widths and height equal to total length (anterior edge of carapace to posterior end of abdomen, exclusive of spinnerets). Measurements were made with the Wild M5 stereomicroscope with ocular micrometer at 12X magnification. Separate regressions for five araneomorph families do not differ significantly in slope and intercept, and the overall regression combining the data for those five families provides a good fit for limited data from two other araneomorph families (Greenstone et al., in press, a). This regression is valid for sticky-trapped as well as directly ethanol preserved specimens (Greenstone et al., in press, b). As the seven families include spiders of varying proportions and shapes, we assumed that mygalomorphs would also fit the overall regression (they certainly do not resemble tetragnathids, the one family which did have a significantly different volume-mass regression).

On April 7, 1984, we were presented with an opportunity to check this assumption partially, when F.A.C. located a group of ballooning *Ummidia* spiderlings near Cullowhee in Jackson County, North Carolina (Coyle 1985). Twenty of these were weighed within 48 h of collection, preserved in 70% ethanol, and mailed to A.-L.H. for measurement. Because these mass determinations and those for the araneomorph volume-mass regressions were made at different times and places, special care was taken in the calibration of both microbalances (a Mettler M5 and Mettler 160, respectively). The twenty *Ummidia* were measured four months after preservation, to ensure that the preserved volumes had come to equilibrium [Araneids require six weeks (Greenstone et al., in press, b)].

RESULTS AND DISCUSSION

Comparison of Estimated Masses of Araneomorphs and Mygalomorphs.—Two hundred sixteen araneomorphs were collected off the soybean field sticky traps and measured. The frequency distribution of their estimated masses is shown in Fig. 1. Means (and standard errors) for mass estimates of the Wake County *Ummidia* and the *S. atlanticus* spiderlings are 3.45 mg (0.13 mg), and 1.25 mg (0.03 mg), with N =9, and 15, respectively, and are indicated by arrows in Fig. 1. Although the araneomorph mass frequency distribution appears representative of other weeks in the summer and fall of 1983 (Greenstone et al., unpublished data), it would be premature to characterize the shape of this distribution in order to derive a parametric assessment of the deviation of mygalomorph balloner masses from those of araneomorphs. However it is clear that the ballooning mygalomorphs studied here are more massive than most other ballooners, and will probably turn out to be in the ninetieth percentile or higher (they are in the ninety-fifth and ninety-eighth in Fig. 1). On the other hand they are not the most massive spiders ballooning. Although we cannot entirely rule out the possibility that some of the larger trapped animals were "rappelling", spiders ranging in mass from 4.8 to 19.2 mg have been trapped by nets suspended more than 100 m above the ground (animals collected by R. A. Farrow in New

South Wales, Greenstone et al., MS in preparation). This suggests that in many mygalomorph taxa ballooning may not be precluded solely or even primarily by large mass.

Although the *Sphodros* and *Ummidia* spiderlings used in this study were not caught in the act of ballooning, we have strong evidence that they were capable of doing so. The age (third instar), time of collection, and behavior of the *S. atlanticus* spiderlings indicate that the animals were overwintering prior to dispersal (see Coyle and Shear 1981 for observations on the phenology of other *Sphodros* spp). Twenty-five of their siblings were kept alive in a glass-topped terrarium containing humid soil. They wandered freely over the soil for a few days and performed pre-ballooning behavior (climbing up the corners of the terrarium and depositing large amounts of silk at the upper ends of the corners just under the glass lid) before finally excavating burrows and constructing their pursewebs. Furthermore the *Sphodros* spiderlings seen ballooning by F.A.C. (Coyle 1983) were almost certainly *S. atlanticus*. The behavior and location of the *Ummidia* spiderlings at the time of collection were also indicative of pre-ballooning behavior.

The twenty spiderlings of *A. unicolor,* the non-ballooning species, had an estimated mean mass of 2.02 mg (standard error =0.19 mg), which is intermediate between those of the two ballooning mygalomorph species. This demonstrates that mass is not the only constraint on ballooning behavior in mygalomorphs and suggests that for at least some species, other factors may be more important than mass in determining whether ballooning occurs. One of us (Greenstone 1982) has suggested that the predictability of the habitat will be the major selective factor in the evolution and maintenance of ballooning behavior, with less predictable habitats selecting for higher rates of ballooning. The habitats of the three species studied here support that hypothesis. *A. unicolor* is most often found in mesic forests (Coyle 1971), whereas the other two species, while sometimes found in forests, are as apt to be found in forest edge habitats, lawns and old fields. Mesic forests are inherently longer lived and hence more predictable than successional habitats like lawns and old fields (Southwood 1962), and they also provide better buffered and hence more predictable microclimates for their inhabitants. It is also possible that the kinds of air currents conducive to mygalomorph ballooning are prohibitively rare in forest habitats.

Comparison of Actual and Estimated Masses of Mygalomorphs.— Measurement of the twenty *Ummidia* spiderlings collected on April 7, 1984, while their siblings were ballooning (Coyle 1985) indicated that the araneomorph volume-mass regression may not be entirely accurate for mygalomorphs. The mean (and standard error) measured mass of this sample was 2.48 mg (0.02), whereas the mean estimated mass was 2.93 mg (0.06). All measured masses were between two and 35% less than those estimated from the volume-mass regression, with a mean deficit of 17.4% (arc-sine transformation of original percent data). If this is representative of the equation's overestimation for all mygalomorphs of this volume range, the arrows in Fig. 1 should be moved to the left one mass class for *Sphodros* and four for *Ummidia:* this does not change their percentile ranks.

The consistent overestimation of *Ummidia* mass by the volume-mass regression is counterintuitive, since the volume estimate does not include the chelicerae and legs, which look more massive in mygalomorphs than in araneomorphs. We can

think of three possible explanations for the overestimation: 1) the regression consistently overestimates the masses of all spiders in this volume range; 2) mygalomorph body shape differs sufficiently from araneomorph body shape that the araneomorph mass-volume regression is not valid for them; 3) mygalomorphs, at least in this volume range, do in fact have lower density than similar sized araneomorphs.

The first possibility was ruled out by comparison of the actual and estimated masses of eight animals (six araneids and two thomisids) from among the 101 used to construct the regression which happened to fall in the same volume range (2.2 to 2.9 mm^3) as the twenty *Ummidia:* exactly half of the estimates were overestimates and half underestimates.

The second possibility will have to be determined by further research. The third is most interesting. If in fact mygalomorph spiderlings are less dense than araneomorphs of the same volume, it may simply reflect some unknown physioanatomical difference unrelated to ballooning. On the other hand such a capacity to be less massive at a given volume could be a preadaptation for the evolution of still lower density to permit ballooning at larger sizes, an ability that might permit the transport of larger energy stores, reduce the rate of body water loss, and enhance colonizing potential by allowing older animals to balloon (MacArthur and Wilson 1967). Given sufficiently strong winds and very long or
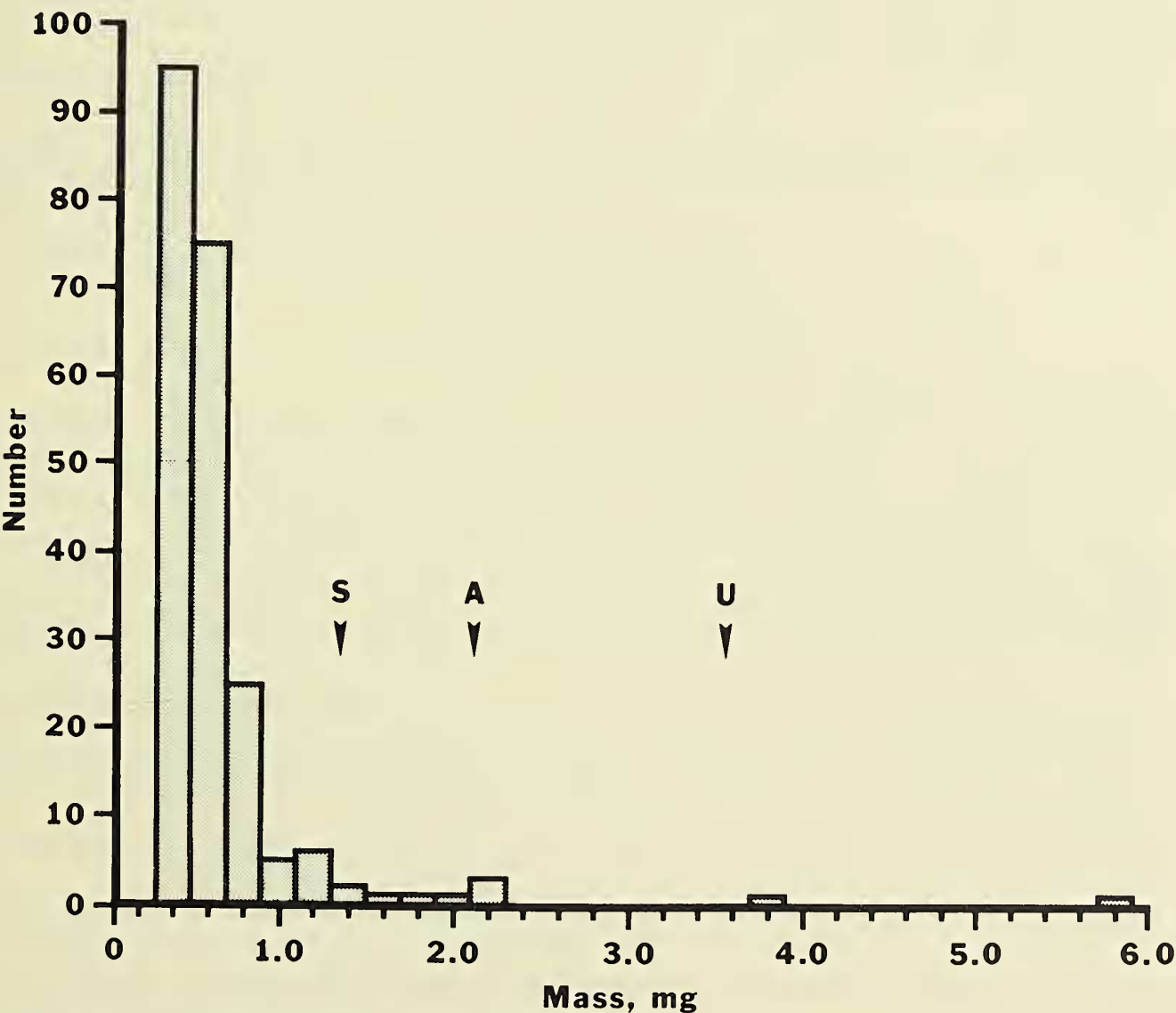

Fig. 1.—Frequency distribution of estimated masses of ballooning araneomorphs collected in a soybean field near Columbia, Missouri, with approximate mean masses of *S. atlanticus* (S), Wake County *Ummidia* (U) and *A. unicolor* (A) spiderlings indicated (arrows). Mass classes are 0.2 mg wide. Class labels designate upper bound of each class.

multi-stranded balloons, spiders much larger than those studied here should be capable of ballooning (R. Buskirk and R. B. Suter, pers. comm.). However, since large spiders seldom balloon, perhaps there is selection against ballooning at large sizes due to such disadvantages as decreased lift resulting from a decreased surface to volume (or mass) ratio, dangerously high terminal velocities, or enhanced visibility to aerial predators. At this point we really do not understand why the distribution of aeronaut masses is so heavily skewed to the light end.

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